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MEDULLOSA OLSENIAE: A PERMIAN MEDULLOSA FROM NORTH CENTRAL TEXAS

BY

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STRUCTURALLY preserved specimens of the Paleozoic seed fern *Medullosa* are represented in considerable abundance in the American mid-continent coal fields, where remains of the plant in the form of stems, petioles and roots are commonly found in the calcareous concretions known as coal balls. Very little information regarding the later Paleozoic development of this interesting and significant group of plants is available from American material, although much phylogenetic theory has been developed recently as the result of studies of its Carboniferous representatives (Baxter, 1949; Stewart, 1951). In view of the possible phylogenetic significance of geologically more recent representatives of *Medullosa*, the specimens comprising this study are described in some detail. To the knowledge of the authors, this description also constitutes the first report of the genus *Medullosa* from post-Carboniferous sediments of North America.

The specimens under consideration were found in section 754, Texan Emigration and Land Company Survey, 10 miles west of Newcastle, Young County, Texas. The material collected consists of fragments of decorticated stems and one petiole. The material occurred *in situ* in

sediments of the Moran Formation, near the base of the Permian system in north central Texas. The seven stem fragments, averaging 4 cm. in length and 2.5 cm. in diameter, are silicified, though with an admixture of calcium carbonate.

The full diameter and exact shape of the stem can only be inferred, owing to the more or less complete decortication which occurred prior to mineralization. In one specimen portions of the inner cortex are retained, though in all specimens there has been partial removal of the woody tissue itself, presumably due to decay and abrasion before petrification.

Medullosa Olseniae,¹ the description and diagnosis of which follows, is a medullosan stem of the "polystelic"² type. It is, however, characterized by the absence of the so-called "star rings" which feature many of the European Permian members of *Medullosa* described by Weber and Sterzel (1896) and subsequently figured by many authors. Our specimens indicate a stem, which, as deduced from the available material, developed a three- to five-membered vascular core, the components of which formed a system of anastomosing vascular bundles, each of which developed a concentric cambium and corresponding secondary xylem. The number of individual

¹ The specific name is given in recognition of Eleanor L. Olsen, wife of the Assistant Preparator of Vertebrate Paleontology of the Museum of Comparative Zoölogy, Harvard University, who collected the specimens in the field and made them available for study.

² The term stele in this discussion is restricted to the primary vascular system of the plant. Inasmuch as the primary vascular system *in toto* is designated stele, the use of the term "polystele" is seemingly illogical. However, usage has tended toward adoption of descriptive anatomical terms derived from living plants even though applied to fossil forms. Until a uniform system of terminology is developed for application to structures of both living and fossil vascular plants, it seems necessary to follow the present conventions in descriptive terminology.

“steles” fluctuates from three to five (Plate LXI, figs. 1 to 9). One specimen exhibits five “steles” throughout its length (Plate LXI, fig. 5); one other shows four “steles” at both ends. One specimen shows three “steles” at one end and four “steles” at the other. Two of the “steles” may be seen to join on the exterior surface. From the appearance of this one specimen there is one stelar fusion per four centimeters of stem length, and it seems reasonable to conclude that the “steles” anastomose throughout the length of the stem, though probably not at regular intervals. The maximum and minimum number of stelar components in *M. Olseniae*, from basal to apical portions of the stem, is not known owing to our fragmentary material. The evidence at hand indicates that the stem of *M. Olseniae* possessed a vascular core of three to five unit “steles,” widely and unevenly spaced around a central parenchymatous core, and in varying degrees of coalescence throughout their vertical extent. Without the attached leaf bases, it is not possible to more than suggest that stelar fusions are associated with the insertions of the leaves.

In *M. Olseniae* the “steles” are more or less elliptical in outline, when seen in transverse sections of the stem, and, collectively, appear to be in elliptical arrangement around the central parenchymatous “pith” (Plate LXIII, figs. 1 and 2; Plate LXI, figs. 1 and 2). It is possible that the unit “steles” were originally arranged in an ellipse and the present more flattened arrangement is due to compression before mineralization. There is no indication of the medullary bundles or “star rings” which constitute such a conspicuous feature of many European species of *Medullosa* (Plate LXII, figs. 8 to 11). The individual stelar units of *M. Olseniae* are from one to three centimeters in cross sectional diameter, along their longer axes. The larger “steles” represent stelar fusions

and their "normal" cross sectional diameter appears to be from one to two centimeters. Each stelar unit is moderately endocentric with respect to the development of secondary wood.

The primary wood, in cross section, consists of an oval to oblong core, comprised of groups of approximately five to fifteen tracheids, each group surrounded by parenchyma, which, in our specimens, is very poorly preserved. The primary xylem clusters are rather evenly distributed throughout the parenchymatous tissue surrounding them. Protoxylem cells of the bundles cannot be distinguished with certainty, though in the better preserved specimens they appear to be mesarch in arrangement.

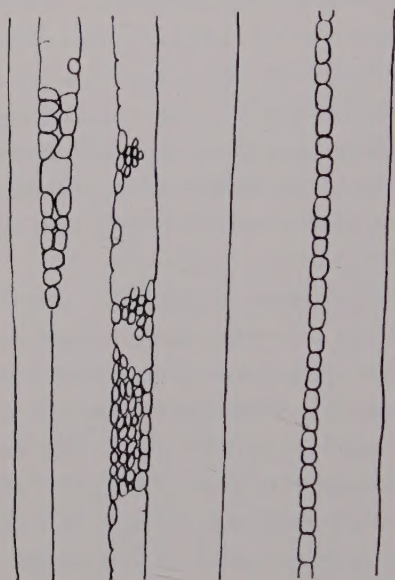
The secondary xylem develops as an eccentric cylinder around each "stele." Unequal cambial activity is evidenced in the greater development of secondary tissue on the inner part of each cylinder, thus producing an endocentric development as found in many Carboniferous species of *Medullosa*. The tracheids are arranged in conspicuous radial rows, usually paired, and each of the double rows is separated by rays of varying width (Plate LXIV, figs. 1, 2 and 3). An interesting feature of the paired radial rows is the alternating position of the individual tracheids with respect to each other (Plate LXIV, fig. 3). This geometric arrangement is probably indicative of extreme apical elongation, or sliding growth, during differentiation of the cambial derivatives in the newly formed secondary wood. It is probably also due in part to changes in spatial relationship of the cells during degradation preceding mineralization. The tracheids are extremely long and of fairly large cross sectional diameter. In the older secondary xylem tracheids range from 80 to 90 μ in diameter, although the outermost cells in several specimens are of smaller size, possibly indicating that the plants had been killed during active secondary growth

before cell enlargement was completed. It seems less likely that an actual diminution of the size of mature cells occurred during ontogeny of the cambium. Alternate, crowded, circular bordered pits occur on the radial walls of the tracheids. The pits on the larger tracheids range from five to six rows on each radial wall (Plate LXIII, fig. 3). The pit orifice, in cells with a sufficiently preserved secondary wall residue, tends to be elliptical with the long axis oriented transversely to the axis of the cell.

Tyloses occur in great abundance within the lumina of the tracheids, and are of the sclerotic type, with thick secondary walls. Tyloses are quite rare in the secondary xylem of living Gymnosperms, although occasionally they occur in roots of conifers. The tyloses of *M. Olseniae* are one of the most conspicuous features in longitudinal sections of the secondary wood, as shown in Plate LXIV, figs. 4 and 5. Despite poor preservation of histological detail in the specimens at hand, it is apparent that they developed by protrusion of the cytoplasm from adjoining ray cells through the bordered pits of adjacent tracheids. Inasmuch as nearly every tracheid was in direct contact with ray cells throughout its length, the capacity for tylose formation can be partially explained. However, the tendency for such outgrowths to develop must have been unusually strong, as evidenced by the formation of a tylose within a tylose as shown in the tracheid figured in Plate LXIV, fig. 6. Such a cytological anomaly as the latter is very difficult to interpret, yet this seems the only explanation for the structure shown.

The rays are poorly preserved and in large part tangentially crushed to an amorphous or alveolar mass of cell wall residues. In better preserved areas the rays are seen to be of two types: uniseriates and very high multi-seriates. The latter are four to six cells in width, of which

the flanking cells are much larger than the cells in the interior of the ray. No conspicuously vertically elongated



TEXT FIG. Tangential section of secondary wood, showing portions of one uniseriate ray and two multiseriate rays. The center ray, as characteristic of the larger rays, is composed of cells of two sizes; the larger along the margin, and the smaller, internal. The outlines of the tracheids, rays, and some of the ray cells were drawn with a camera lucida. Other ray cells were drawn by direct comparison with the thin section. $\times 50$.

cells can be observed either in the uniseriate rays or at the margins of the multiseriates (Text Fig.).

Cells of the cambium are not visible, but the phloem tissue is preserved in some areas. The sieve elements are crushed, but appear as double or triple rows between the flaring phloem rays (Plate LXIV, fig. 1).

As noted, very little of the cortex was preserved, and leaf traces were not seen. A single row of sclerotic strands, just outside the phloem region, extends around the secondary body of each woody cylinder. There is no evidence of internally developed periderm.

Diagnosis

Medullosa Olseniae Roberts & Barghoorn sp. nov.

A stem, elliptical in cross sectional outline, approximately two \times four cm. in diameter at outer margins of the "polystele." The "polystele" consists of three to

five "steles" arranged concentrically around a central parenchymatous core. "Steles," including the surrounding secondary wood, elliptical in outline in transverse section, and varying from one to three cm. along the long axis. Secondary xylem forming a concentric cylinder around each "stele," but, to a moderate degree, endocentrically developed. "Star rings" and accessory internal bundles absent. Primary wood arranged in small aggregates, or scattered bundles surrounded by parenchyma. Secondary wood consists of tracheids and rays. Tracheids large, with closely spaced circular bordered pits on the radial walls. Rays very abundant and of two types: uniseriate and multiseriate, the latter four to six cells in width. The rays flare conspicuously in the phloem.

Locality and horizon: Lower Permian, Moran Formation, Section 754, Texan Emigration and Land Company Survey, 10 miles west of Newcastle, Young County, Texas.

Collected by: Eleanor L. Olsen.

Material: Seven silicified stem fragments.

Type: Seven stem fragments and 7 ground sections in the Paleobotanical Collections of Harvard University, No. 50,001 to 50,007.

Discussion

The specimens under consideration clearly conform to the definition of the genus *Medullosa* in possessing "poly-stelic" structure, with each stelar component developing, independently, its own cylinder of secondary tissues. The known members of the genus may be divided into three geographic and stratigraphic categories: 1) species of the European (German) Permian; 2) species of the European Carboniferous; and 3) species of the American Carboniferous (chiefly mid-Pennsylvanian?).

Comparison of the stelar patterns and stem structure of the European Permian forms (Plate LXII, figs. 8 to 11) with *M. Olseniae* rules out any close relationship. The former are all characterized by elongated and peripherally

arranged "steles," with "star rings" in the central parenchymatous region, and in some forms successive cambia in the cortical zone. These forms are far more complex than *M. Olseniae*, and, indeed, represent some of the most bizarre modifications of vascular tissue among Paleozoic plants.

Comparison of the new species must therefore be made with forms described from the European and American Carboniferous. In many respects *M. Olseniae* is within the range of variation of the Carboniferous forms, especially in anatomical details, such as tracheary pitting, size of the stelar units, endocentricity of the secondary cylinders, and structure of the rays. Differences in the structural variation of these anatomical features comprise the primary basis for establishment of several species of American forms, although these differences may actually be merely structural variables of the same species. In the absence of more complete material from a single plant, however, the establishment of species categories based on anatomical differences in fragmentary specimens seems the only reasonable procedure in the taxonomic treatment of Paleozoic plants and other extinct groups of plants. On the basis of the structure of the primary xylem and of the secondary xylem, *M. Olseniae* differs in no fundamental way from the carboniferous forms. If the number of component "steles" in the "polystele" is considered a basic taxonomic character in *Medullosa* (which may reasonably be questioned in certain cases), *M. Olseniae* differs from previously described forms in that it consistently possesses three to five "steles." Carboniferous forms described in the literature may be grouped into two major categories: 1) those with two to four "steles"; and 2) those with six to eight "steles." In the first group those with two "steles" are *M. distelica* Schopf (1939) and *M. pandurata* Stewart (1951);

those with three are *M. anglica* Scott (1899), *M. Thompsonii* Andrews (1945), *M. endocentrica* Baxter (1949), *M. pusilla* Scott (1914), *M. elongata* Baxter (1949) and *M. Noei* Steidtmann (1944); and that with four "steles" is *M. centrofilis* De Fraine (1914). The latter species is curious in possessing one small "star ring," flanked by three larger "steles" (Plate LXII, fig. 2). The second group consists of one form only, *M. primaeva* Baxter (1949), which possesses six to eight "steles" of varying size (Plate LXII, fig. 3).

In addition to exhibiting a presumably significant difference in the number of unit "steles," *M. Olseniae* presents a perhaps more significant character in the possession of a central parenchymatous core devoid of "star rings" or other supernumerary vascular strands. Because of these two structural features, it seems desirable to propose a new specific name for the *Medullosa* described in this study.

Owing to its occurrence in post-Carboniferous sediments, *M. Olseniae* is of interest in the interpretation of phylogenetic trends in the Medullosan group. In comparison with Permian representatives in western Europe it is surprisingly simple in structure, and may be interpreted as structurally more primitive. However, it is difficult to incorporate *M. Olseniae* into the phylogenetic schemes proposed for the American Carboniferous forms by Baxter (1949) and Stewart (1951). Until more is known of the possible variation within a single "species" of *Medullosa*, however, phylogenetic schemes will probably require periodic modification.

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ILLUSTRATIONS

EXPLANATION OF THE ILLUSTRATION

PLATE LXI. Stelar organization in the genus *Medullosa*. Figs. 1-9, *Medullosa Olseniae*; figs. 10, 11, Carboniferous species.

Fig. 1. Reconstruction of the vascular system of *M. Olseniae*, showing the flat ring of "steles," based on specimen diagrammed in fig. 5, and oriented similarly. The crushed internal parenchyma has been restored to its assumed dimensions. $\times 1.5$

Fig. 2. Reconstruction of the vascular system in another specimen of *M. Olseniae*, based on the specimen drawn in fig. 4, and oriented similarly. The largest "stele" appears to be the result of the fusion of two. (See fig. 6 and 7.) $\times 1.5$

Fig. 3. Drawing of the specimen diagrammed in figs. 6 and 7, to show the appearance of the fossils. (See fig. 7.) $\times 1.5$

Fig. 4. Stelar organization of the one specimen which shows uncrushed internal parenchyma. (See Plate LXIII, fig. 1) $\times 1.5$

Fig. 5. Diagram of the specimen containing portions of five "steles." (See Plate LXIII, fig. 2.) $\times 1.5$

Fig. 6. Appearance of one end of specimen which shows a stelar fusion. Steles 3 and 4 are separate. $\times 1.5$

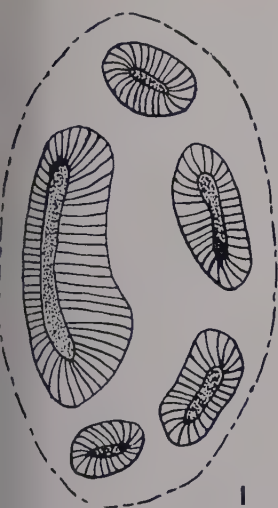
Fig. 7. Appearance of the other end of the specimen drawn in fig. 6. Steles 3 and 4 have fused. $\times 1.5$

Fig. 8. A less complete specimen of *M. Olseniae*, which shows secondary wood on both sides of the primary body. $\times 1.5$

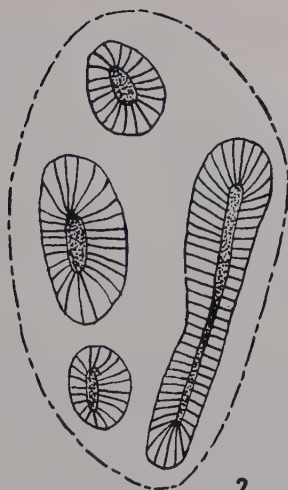
Fig. 9. Another specimen of *M. Olseniae*, which contains a virtually complete "stele." $\times 1.5$

Fig. 10. *M. pusilla* Scott. From Baxter, after Andrews. $\times 1.8$

Fig. 11. *M. distelica* Schopf. From Baxter, after Andrews. $\times 1.8$



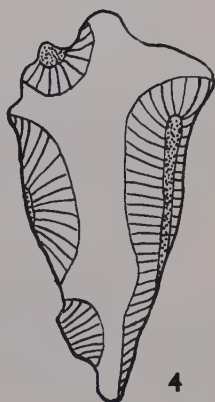
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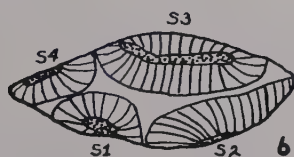
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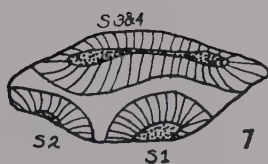
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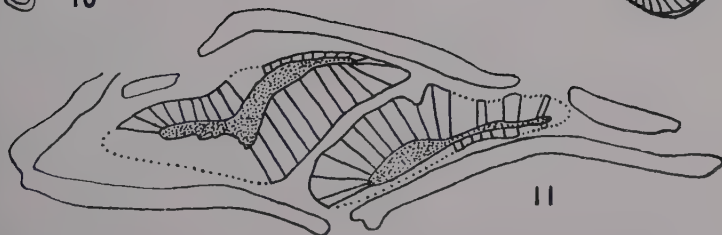
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EXPLANATION OF THE ILLUSTRATION

PLATE LXII. Stelar organization in the genus *Medullosa*, continued.

Figs. 1-7. Carboniferous species. These, with the addition of those figured on Plate LXI, figs. 10 and 11, represent all the known Carboniferous species, with the exception of *M. Noei*. The stelar pattern of *M. Noei* does not resemble that of *M. Olseniae*, and is omitted from the figures because of its large size. Figs. 8-11 show the known Permian species from Germany.

Fig. 1. *M. elongata* Baxter. From Baxter. $\times 1.8$

Fig. 2. *M. ventrifilis* De Fraine. From Baxter, after Andrews. $\times 1.8$

Fig. 3. *M. primaeva* Baxter. From Baxter. $\times 1.8$

Fig. 4. *M. anglica* Scott. From Baxter, after Andrews. $\times 0.75$

Fig. 5. *M. endrocentrica* Baxter. From Baxter. $\times 1.8$

Fig. 6. *M. pandurata* Stewart. From Stewart. $\times 0.70$

Fig. 7. *M. Thompsonii* Andrews. From Baxter, after Andrews. $\times 1.8$

Fig. 8. *M. Leuckartii* Göppert and Sterzel. This and the following diagrams show the characteristic peripheral "steles" and accessory secondary woody cylinders with included "star rings" which are found in the Permian species. This stelar organization is more complex than is found in the Carboniferous species, and is clearly more specialized. From Weber and Sterzel. $\times 0.75$

Fig. 9. *M. porosa* Cotta. From Weber and Sterzel. $\times 0.75$

Fig. 10. *M. stellata* Cotta. From Weber and Sterzel. $\times 0.75$

Fig. 11. *M. Solmsii* Schenk. From Weber and Sterzel. $\times 0.75$

PLATE LXII



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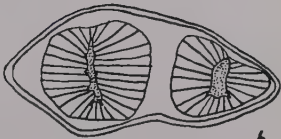
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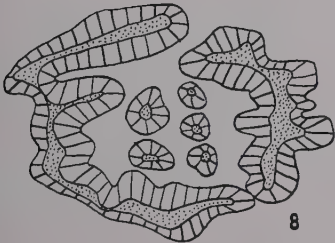
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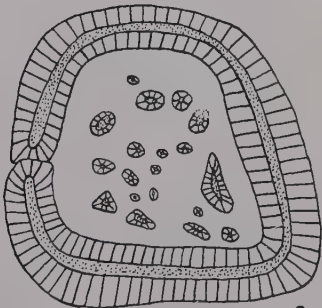
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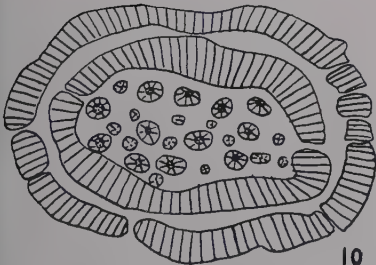
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EXPLANATION OF THE ILLUSTRATION

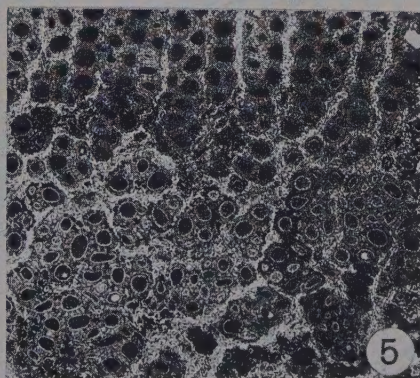
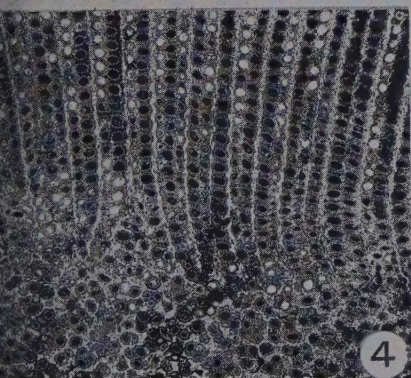
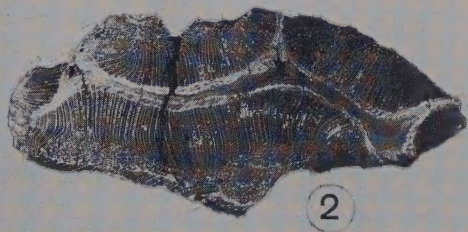
PLATE LXIII. Fig. 1. Transverse section of *M. Olseniae*, showing specimen with portions of four "steles" grouped around the central core of parenchyma. Note arcs of internally developed phloem. $\times 1.5$

Fig. 2. Transverse section of *M. Olseniae*, showing portions of five "steles" and the crushed central parenchymatous core. $\times 1.5$

Fig. 3. Radial longitudinal section of *M. Olseniae*, showing the alternate multiseriate circular bordered pits on the radial wall of a tracheid. $\times 115$

Fig. 4. Transverse section, showing innermost secondary xylem and part of the primary wood of a "stele." The lumina of the tracheids of both primary and secondary xylem are filled with a black amorphous substance, partially organic and partially mineral. $\times 25$

Fig. 5. Same section as fig. 4, but more highly magnified. Note the aggregates of primary xylem tracheids interspersed with irregular areas of crushed parenchyma cells. $\times 35$



EXPLANATION OF THE ILLUSTRATION

PLATE LXIV. Sections of the secondary xylem of *Medullosa Olseniae*.

Fig. 1. Transverse section showing the outermost secondary xylem and the phloem of one of the "steles." Note the radial rows of sieve elements (light) and the flaring rays of the phloem (dark) in the upper third of the figure. $\times 20$

Fig. 2. Transverse section showing radial rows of tracheids separated by multiseriate rays of crushed cells. The lumena of the tracheids are black. $\times 60$

Fig. 3. Same section shown in fig. 2, but more highly magnified. Note the multiseriate rays separating the double rows of alternately spaced tracheids. The black contents of the lumena are in sharp contrast to the bright layers of the inner tracheid wall and the pit chambers, the latter represented by bright beads. $\times 115$

Fig. 4. Tangential longitudinal section showing the long tylose filled tracheids and closely spaced crushed rays of the secondary xylem. $\times 25$

Fig. 5. Same section shown in fig. 4, but more highly magnified. The poor preservation of the rays is evident in the amorphous appearance of tissue between the tracheids. Note tyloses in the tracheids. $\times 60$

Fig. 6. Same section shown in fig. 4, but more highly magnified. The spherical structure in the center of the figure is a tylose which apparently developed within the pre-existing tylose of the tracheid. That the structure shown is organic and a part of the plant tissue is evident by the similarity in its optical properties with those of the surrounding cell wall residues. The upper wall of the primary tylose is represented by the rounded cell wall in the lumen of the tracheid in the upper part of the figure. $\times 260$

PLATE LXIV

